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AN ECOLOGICAL STUDY OF

THE BUTTERFLIES OF THE SIERRA DE TUXTLA

IN VERACRUZ, MEXICO[1]

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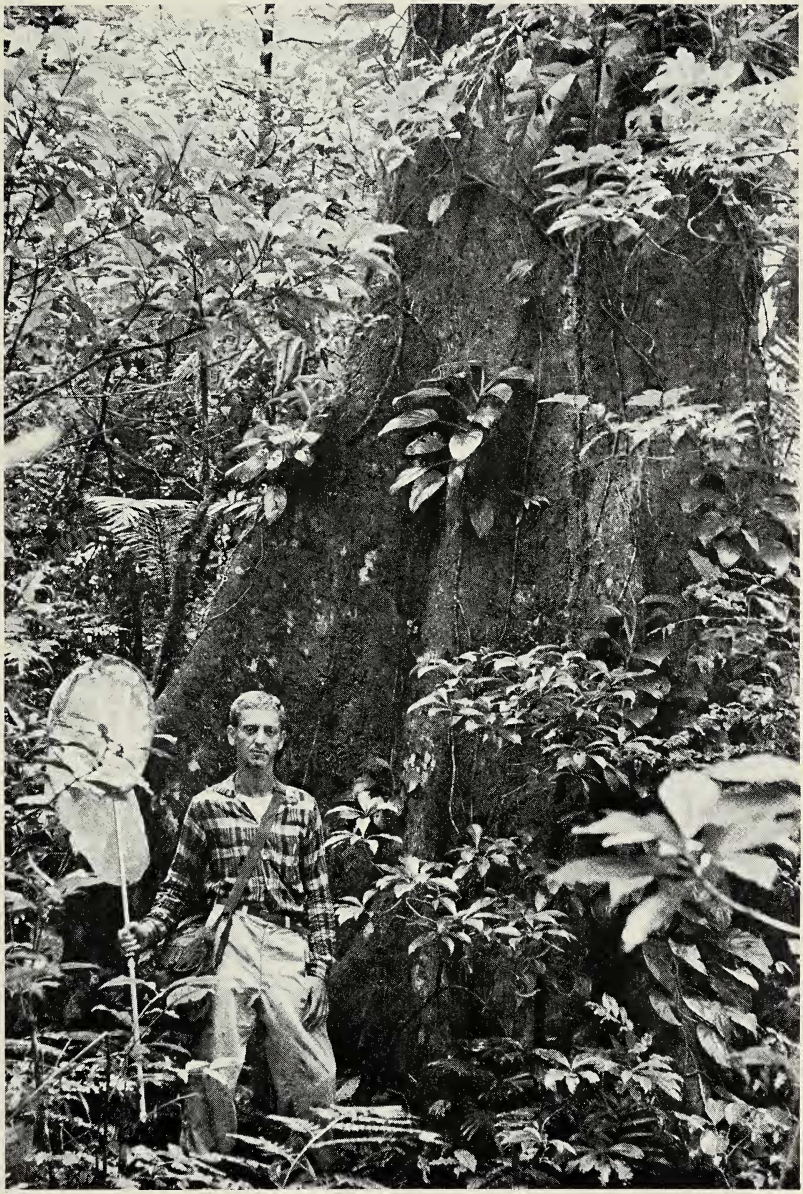

FRONTISPIECE
Author in Montane Rain Forest on Volcán San Martín Tuxtla. August 1962, 3,500 feet. Photograph by R. F. Andrle.

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ABSTRACT

The Sierra de Tuxtla is a small and isolated volcanic mountain range along the Gulf coast of southern Veracruz, Mexico. Because of the geographic isolation, the range affords excellent conditions for distributional and ecological investigations. The present study is the first comprehensive report of the butterfly fauna of the range or for any geographic unit within the Neotropics.

Fifteen months (representing all seasons of the year) were spent in the field during 1962, 1963, and 1965. The various relatively widespread plant communities were classified into 16 distinct types or formations. All of these formations were sampled for butterflies and a total of 3,893 specimens representing 359 species, 133 genera, and eight families were collected. Of these species, 40 are recorded from the Sierra for the first time; these include ten range extensions within the state of Veracruz, 18 new state records, nine new national records, three new species, and one new subspecies. All 359 species are listed in the species accounts along with the field data—complete (number of specimens, locales and altitudes, and collection date) for those species that represent new records for the Sierra but condensed (number of specimens and only ranges in altitude and collection dates) for those species recorded previously from the Sierra.

Various relationships between the butterfly fauna and the environment are discussed. First, an analysis of the plant formations with their indicator and characteristic butterfly species indicates that life zone boundaries within the Sierra are vague but still definable. The Sierra can be divided into two major zones—an Upper Tropical Zone and a Lower Tropical Zone. Furthermore, the data indicate that the Lower Tropical Zone can be subdivided into a humid and an arid component.

Second, the majority of the butterfly species were found in the Lower Tropical Zone in the open and relatively open plant formations whereas very few species (principally members of the Ithomiidae and Satyridae) were found in the dark interiors of the forests. Because of the Sierra's relatively low altitude and relatively uniform rainfall, it is suggested that the principal governing factor determining butterfly areal and altitudinal distributions is the plant formation.

Third, although butterfly zoogeography is not sufficiently advanced to enable one to determine the origins of most genera and species groups, the majority of the genera (97%) and species (97%) found within the Sierra's boundaries appear to have their affinities with forms further south; consequently, the butterfly fauna is essentially Neotropical.

Fourth, although the climate in the Sierra is relatively mild and uniform, enough diversity exists to produce significant variations in the butterfly populations. In general, populations of most species reached maximum densities in late summer and early fall and their minimum densities in winter and spring. In addition, daily population densities were greatest between the hours of 10:00 A.M. and noon.

Fifth, butterfly endemism proved to be comparable to endemism in other groups; three species, one subspecies, and one form (probably a good subspecies) are endemic to the Sierra de Tuxtla.

I. INTRODUCTION

The Sierra de Tuxtla or Tuxtla Mountains (Tuxtla being the Spanish corruption of the Axtec "Toxtli" meaning rabbit) is a rather restricted highland of volcanic origin situated between 18°10′ and 18°45′ N latitude and 94°42′ and 95°27′ W longitude on the Gulf Coastal Plain of the state of Veracruz in the Republic of México (Fig. 1). The range trends northwest-southeast with areal dimensions of approximately 55 by 30 miles and is isolated from any other highland (the nearest being the Sierra Juarez in the state of Oaxaca approximately 90 miles away) by the Veracruz lowlands, principally the drainage basins of the Papaloapan and Coatzacoalcos rivers. The Sierra is composed of numerous ridges and volcanic cones and peaks of which four attain elevations in excess of 3,000 feet, the maximum elevation being 5,450 feet. These volcanic extrusions encircle a central basin containing the picturesque Lago Catemaco, the third largest lake in Mexico (Plate 1).

When man first entered and began to settle the Sierra is still unknown. Sears (1952) states that artifacts dating from approximately 1500 to 500 B.C. and probably Olmec in origin were found in archcological sites in and around the range. The Spanish reached the Sierra a few years subsequent to their arrival in Mexico—ca. 1522 (Melgarejo Vivanco, 1960). Today the area of approximately 2,700 square miles is moderately populated with both Mexicans and Indians, (Popolucas and Aztecs), the total population in 1960 being approximately 145,000 (Andrle, 1964). The people are engaged mainly in subsistence agriculture, which includes the cultivation of corn, coffee, tobacco, and citrus fruits. Because of the rather long history of settlement and cultivation, relatively few undisturbed areas still exist. These are found principally on the windward (Gulf facing) slopes of the major volcanoes and on the leeward slopes above elevations of 2,500 to 3,000 feet.

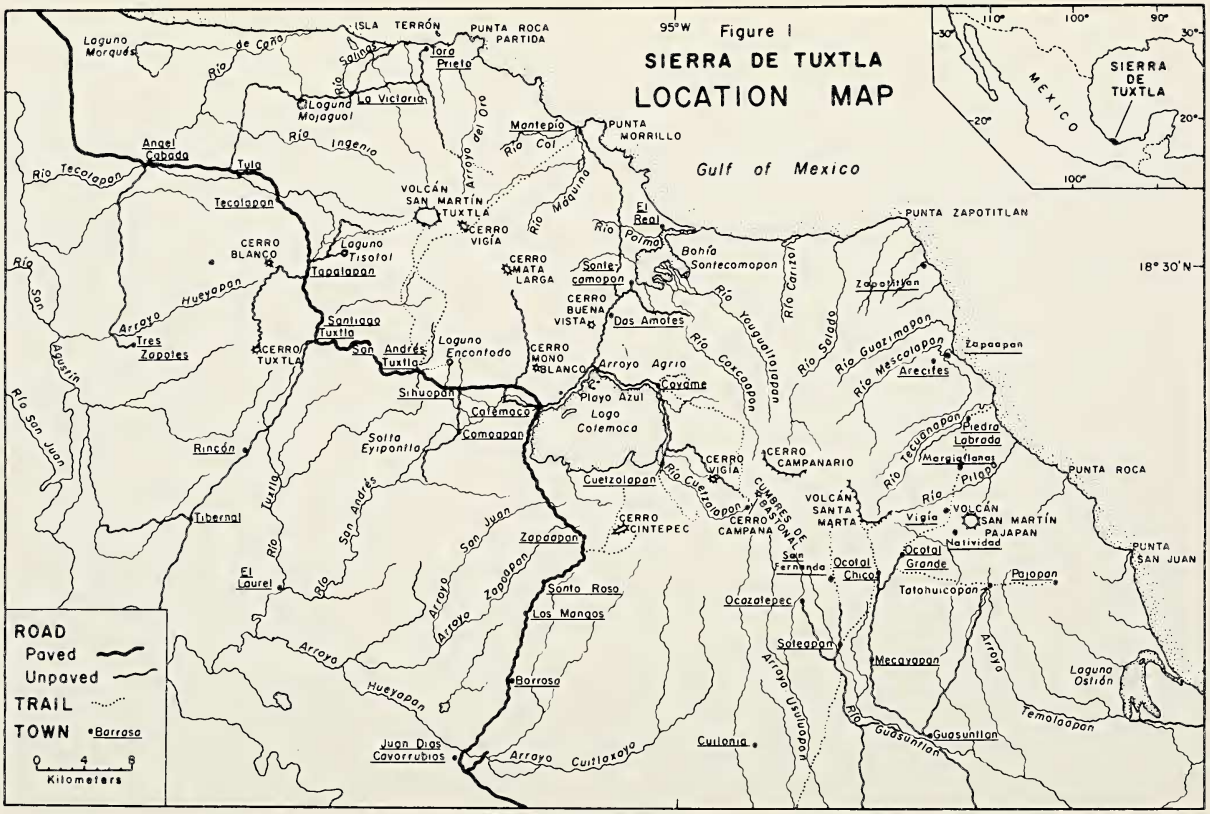

FIGURE 1
Location map of the Sierra de Tuxtla. Map modified from that of Andrle (1964). Basic map used with the permission of the author.

Scientific studies in the Sierra have been very limited and brief; biological investigations have been confined almost exclusively to the vertebrate fauna of the Lago Catemaco basin and the slopes of Volcán San Martín Tuxtla. Avian and mammalian studies include those of Sclater (1897), Wetmore (1943), Goldman (1951), Davis (1952), Amadon and Eckelberry (1955), Edwards and Tashian (1959), and Andrle (1964). Herpetological studies include those of Firschen (1950), Firschen and Smith (1956), and Pyburn (1963, 1964, 1966). Previous studies on arthropods are limited to a single paper on opilionids (Goodnight and Goodnight, 1959).

My interest in the Sierra de Tuxtla began in 1961 because of R. F. Andrle, a fellow graduate student who previously had visited the range and who at the time was preparing for a 12 month return visit in early 1962 to study in detail the mammalian and avian faunas. Andrle's enthusiasm about the Sierra coupled with the fact that comprehensive studies on the bionomics of Neotropical butterflies are practically nonexistent, convinced me that the Sierra de Tuxtla would be an ideal study area for me. So in June 1962 and with Andrle as a field partner, I began my investigation of the Sierra's butterfly fauna. During this first study period (June through mid-December) my main base of operations was located at Playa Azul on Lago Catemaco. From that locale I directed my studies to the Volcán San Martín Tuxtla massif and the Lago Catemaco-Bahía Sontecomapan areas. Two incidental papers (Ross, 1963, 1964b) resulted from this endeavor. The following year, June through August 1963, I made a return visit to the Sierra and established a base at Ocotal Chico. During this period my studies were directed to the Volcán Santa Marta massif. Three incidental papers (Ross, 1964c, 1964d; Hepburn and Ross, 1964) resulted from this study. In 1965 (February through July) I revisited the Ocotal Chico site and expanded my investigation of the region to include the Volcán San Martín Pajapan massif. One incidental paper resulted from this 1965 trip (Ross, 1966). Transportation during all of the study periods was provided by four-wheel drive vehicles, trucks, mules, power boats, canoes, and my own two feet.

This dissertation is based on an assemblage of 3893 butterfly specimens collected during a total of 15 months of personal field

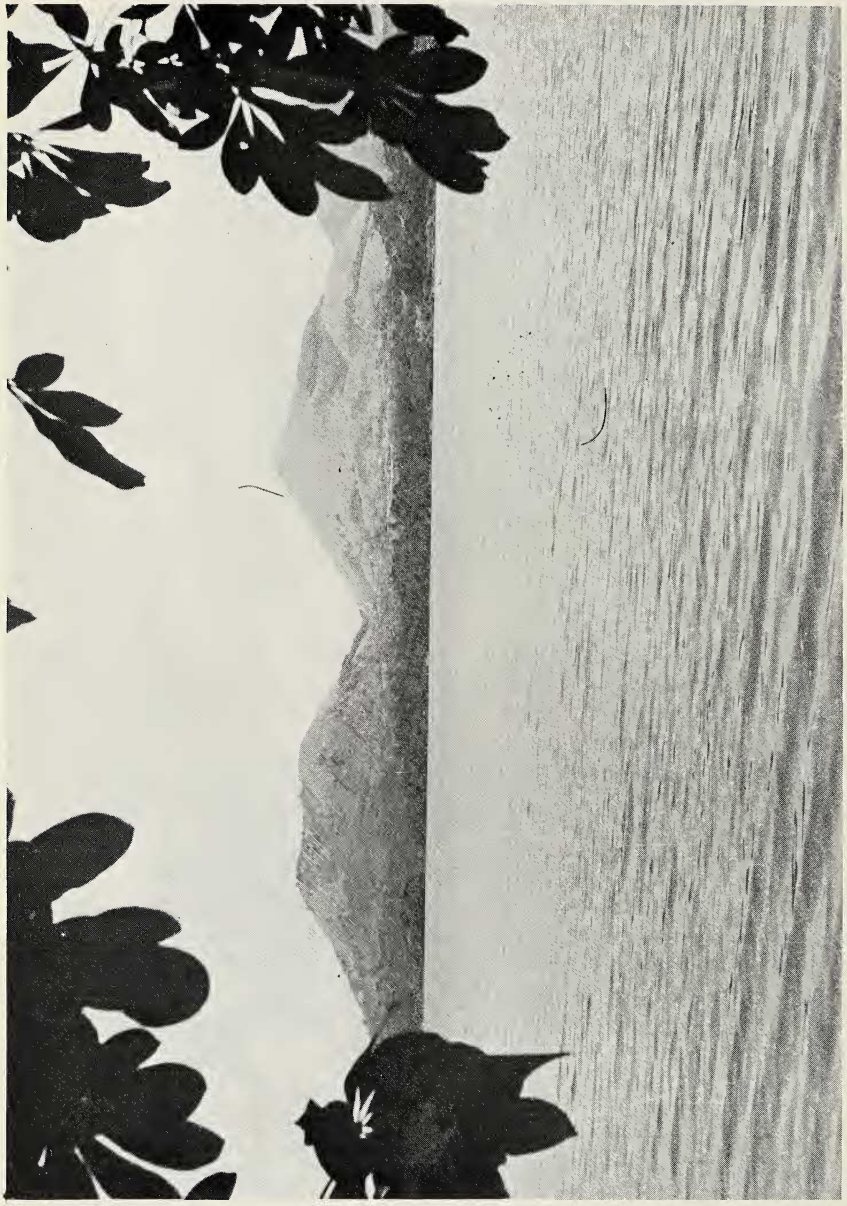

PLATE 1
Lago Catemaco, view toward the western margin. August 1962, 1,100 feet.
Photograph by R. F. Andrle.

work in the Sierra. In sections II (TOPOGRAPHY AND GEOLOGY) and III (CLIMATE) I have relied heavily on information presented by Andrle (1964) and the reader is referred to that work for additional and more detailed discussions of those topics.

II. TOPOGRAPHY AND GEOLOGY

The Sierra de Tuxtla is an isolated mountain mass dominated by four relatively large volcanoes. To the north these slope rather steeply down to the Gulf of Mexico. To the South, West, and East they slope more gently down to the Gulf Coastal Plain. All slopes are deeply dissected and a radial erosion pattern is very evident. The Sierra can be divided by the basin of Lago Catemaco into a northwest and a southeast massif. The northwest massif is dominated by Volcán San Martín Tuxtla (5,450 feet; Plate 2) and to a lesser extent by Cerro Tuxtla (2,725 feet), Cerro Blanco (2,375 feet), and the elongate Cerro Cintepec (2,950 feet). Numerous small cones, hills, and crater lakes are common south, east, and west of Volcán San Martín Tuxtla. To the north, long, steep-sided ridges radiate down to the Gulf of Mexico. The southeast massif is dominated by Volcán Santa Marta (5,250 feet; Plate 3), Volcán San Martín Pajapan (3,750 feet; Plate 4), and Cerro Campanario (3,900 feet). The southeast section exhibits more uniformity than does the northwest section in the sense that there are very few secondary cones and crater lakes.

The numerous ravines on the slopes of the volcanoes usually contain swift-flowing, clear streams, the flow from many of which is either significantly reduced or stopped during the spring dry season. The streams usually are fed by cool, clear springs that issue from rock crevices on the upper slopes of the volcanoes. At lower elevations the streams join larger streams and rivers which in turn eventually flow into the Gulf of Mexico.

Murray (1961) states that the Tuxtla Uplift probably existed as early as Mesozoic times. He considers the uplift to be high areas of basement rock in the Mesozoic-Cenozoic geosyncline that probably was part of the arc-shaped "Tamoulipas-Yucatan archipelago." Later, this syncline sank and was subjected to Cretaceous and Tertiary deposits of blue clays and shales, tuffs, sandstones, limestones, and conglomerates, which upon later emergence of the Sierra, were partially eroded away.

Schieferdecker and Tschopp (1922) suggest that the Sierra

PLATE 2
Volcán San Martín Tuxtla. August 1962, 2,000 feet. Photograph by R. F. Andrle.

rests on a diaritic laccolith of early Miocene or Oligocene age that lifted and in places folded the Tertiary beds and from which the volcanic extrusions have emerged. These extrusions comprise most of the present-day Sierra and consist of older Pliocene deposits of an acid andesitic character upon which were superimposed basalt flows and volcanic plugs of late Pliocene age following the last marine inundation.

Andrle (1964) recognized seven principal eruption centers or zones within the Sierra. These are: Cerro Tuxtla, Cerro Blanco, Volcán San Martín Tuxtla, the Lago Catemaco Basin (including Cerros Mono Blanco, Las Animas, and Cintepec), Cerro Campanario, Volcán Santa Marta, and Volcán San Martín Pajapan. Besides these principal cerros, there are numerous subsidiary lava, ash, and cinder cones in the area, principally in the vicinity of Volcán San Martín Tuxtla. The true nature of Lago Catemaco is still debatable. Friedlaender (1923) considered it to be a caldera but Andrle (1964) suggests that it is simply a spring and stream-filled low section of the range whose southern and western borders are effectively blocked by volcanic cones and debris. Layers of ash, lapilli, and cinders are evident particularly in the Catemaco basin. Basalt bombs, pumice, and asphalt cakes are fairly common, particularly along the coast. Fine-grained olivine basalt rocks are the dominant rock type throughout the Sierra. These are evident as blocks, both large and small, and as extensive flows, which in places exhibit columnar faulting.

Only Volcán San Martín Tuxtla has a historical record of eruptions. This fact tends to support the suggestions of Friedlaender (1923) that the northwest massif is of younger geologic age than the southeast counterpart. Medel & Alvarado (1963) briefly described an eruption on October 15, 1664, which Friedlaender (1923) defined as an ash eruption with a possible restricted lava flow to the north. Mociño (1870) reported a second eruption that began in March 2, 1793 and that consisted of violent explosions, lava flows to the northeast and northwest, and ash falls that continued intermittently through September. Garcia (1835) observed fumarolic activity in the crater in 1829 but nothing more.

PLATE 3
Volcán Santa Marta. Body of water in the foreground is an artificially created reservoir. June 1965, 500 feet.

The four major volcanoes each show well developed oval and steep-walled craters, which for the most part, are open to the north indicating the direction of major lava flows. The crater of Volcán San Martín Tuxtla has a maximum length of approximately one mile and a maximum depth of approximately 600 feet. The crater of Volcán Santa Marta has a maximum length of approximately one and a half miles and a maximum depth of approximately 500 feet. Cerro Campanario and Volcán San Martín Pajapan have craters smaller and shallower than those of Volcáns San Martín Tuxtla and Santa Marta.

III. CLIMATE

The Sierra de Tuxtla is characterized by rather uniform year-round temperatures and seasonal rainfall. This rather mild climate is a result of the moderating effect of the Gulf of Mexico. Andrle (1964) lists temperature and precipitation data for six stations in the Sierra. Unfortunately, all of these stations are in a relatively narrow zone on the southern slopes of the Sierra and hence, the data can be used only to illustrate general trends. April and May usually are the warmest months and January and February the coolest. The average annual temperature is approximately 75.5°F (average elevation of 955 feet). The average mean for the coldest month is 68°F. The lowest temperature recorded at any station (San Andrés Tuxtla, 1,188 feet, 32 years of data) was 44.2°F. Medel & Alvarado (1963) reported that on February 9 and 10, 1899, the peak of Volcán San Martín Tuxtla was covered with ice; thus freezing conditions are not unknown on the peaks of the highest volcanoes. Low temperatures usually occur between October and April after the passage of a mass of cold air that moves across the Gulf from the north or northeast. These fronts, which are called "nortes" by the local inhabitants, vary in intensity and duration, some being weak and lasting for only two or three days, others somewhat stronger and lasting for as long as seven days.

Precipitation is variable with two pronounced seasons—a wet season from June through January (maximum rainfall in July and October) with usually a slight decrease in August, and a dry season from February through May (minimum rainfall in March and April). Most precipitation during the winter months is associated with the passage of fronts. Most summer and fall precipitation occurs during thundershowers in the night and early morning. Andrle's climatic data indicate that rainfall is

PLATE 4
Volcán San Martín Pajapan. May 1965, 2,600 feet.

principally an orographic type and varies considerably between each station and even from year to year at any single station. The minimal early average for any station is 69 inches at Guasuntlan (elevation 595 feet) and the maximal yearly average is 163 inches at Coyame (elevation 1,122 feet). Rainfall above elevations of 1,500 feet on the Gulf slopes is probably in excess of 170 inches per year, and the peaks of the principal volcanoes conceivably receive upwards of 200 inches per year because of the orographic effect.

The cloudiest months are December, January, and July; the least cloudy are March, April, and May.

Since the mean temperature of the coldest month is greater than 64.4°F and the mean precipitation of the driest month is greater than 2.4 inches, the Sierra falls within the "Tropical Rain Forest Climate" (Af) of Koppen (1936).

IV. VEGETATION

The Sierra de Tuxtla lies within (but near the northern border of) the Neotropical Realm of Wallace (1876) and represents the most northern extension of the relatively uninterrupted belt of tropical rain forest that extends (in climatically favorable areas) from southern Mexico through Central America and far into South America (Leopold, 1950; 1959). Hence the floristic composition of the region is basically tropical with most components being related to plant groups further south. This tropical composition coupled with the fact that the Sierra represents a relatively small geographic area (approximately 2,700 square miles) would lead one to the conclusion that the flora of the region is rather homogeneous. Such a conclusion, however, would be completely erroneous because the Sierra exhibits a considerable diversification in vegetation. This diversity is a result of many factors of which some of the most important include: altitudinal zonation from sea level to a maximum elevation of 5,450 feet resulting in temperature and rainfall gradients; differences in the composition and ages of soils due to differential weathering and variances in age of parent material; the long axis of the range in respect to the prevailing winds resulting in relatively heavy precipitation on the Gulf facing slopes and a slight rain shadow effect on the leeward slopes; and

the agricultural practices of man resulting in the presence of all stages of plant succession.

Plant Formations

In attempting to define the habitats of butterfly species in the Sierra, a more subtle ecological division that either "life zone" or "biotic province" had to be chosen. Because of the Sierra's numerous and frequently widely distributed plant communities, I decided to empoly a habitat classification based on plant formations.

Andrle (1964) in his investigation of the Sierra differentiated between ten distinct types of vegetation. However, because of the broadness of many of his terms I have found it necessary to modify this classification. This was accomplished by correlating (where possible) the apparent climax types with those as outlined by Beard (1944; 1955). When no correlations were apparent, e.g., the various seral communities and the oak and pine communities, I have errected new categories, being careful not to employ any of the Beard terminology. The result of this effort is that I recognize 16 distinct formations in the Sierra (Table 1). The geographic locations of the major types are illustrated in Figure 2. In actuality the boundaries between each type and the next are rather arbitrary for oftentimes relatively wide transitional zones or ecotones exist between formations.

(to be continued)